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Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests

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ABSTRACT

1. Climate change is driving a redistribution of species and reconfiguration of ecological communities at a global scale. Persistent warming in many regions has caused species to extend their geographical ranges into new habitats, with thermally-tolerant species often becoming competitively dominant over species with colder affinities. Although these climate-driven changes in species abundance and diversity are well documented, their ecosystem-level implications are poorly understood, and resolving whether reconfigured communities can maintain fundamental ecosystem functions represents a pressing challenge in an increasingly warmer world.
2. Here, we investigated how climate-driven substitutions of foundation species influence processes associated with carbon and nutrient cycling (biomass production, detritus flow, herbivory, decomposition) by comparing two habitat-forming kelp species with contrasting thermal affinities. We examined the wider ecosystem consequences of such shifts for the observed (and predicted) emergence of novel marine forest communities in the NE Atlantic, which are expected to become more dominated by range-expanding, warm-temperate kelp species.
3. Warm-temperate kelps both accumulated and released 80% more biomass than the cold-temperate species despite being taxonomically closely-related and morphologically similar. Furthermore, the warm-temperate species accumulated biomass and released detritus year-round, whereas the cold-temperate species did so during short, discrete periods. The warm-temperate kelps supported higher densities of invertebrate grazers and were a preferred food source. Finally, their detritus decomposed 6.5 times faster, despite supporting comparable numbers of detritivores. Overall, our results indicate an important shift in the cycling of organic matter along large sections of NE Atlantic coastline following the climate-driven expansion of a warm-affinity kelp, with novel forests supplying large amounts of temporally-continuous—yet highly labile—organic matter.

4. Synthesis. Collectively, our results show that, like species invasions, climate-driven range expansions and consequent shifts in the identity of dominant species can modify a wide range of important ecosystem processes. However, alterations in overall ecosystem functioning may be relatively limited where foundation species share similar ecological and functional traits.

KEYWORDS

Temperate reefs, range expansion, range shift, climate change, Laminariales, macrophyte, novel ecosystems, *Laminaria ochroleuca*, *Laminaria hyperborea*

INTRODUCTION

Humans have increasingly impacted the natural environment over the last five millennia (Bell & Walker 2004), to the point where very few contemporary ecosystems are free from human influence (Ellis *et al.* 2010). Human activities have led to the reorganization of biological communities worldwide, principally by (i) introducing individuals and populations beyond species' native ranges; (ii) driving species extinctions; and (iii) altering key environmental factors that constrain species distributions, thereby inducing species range shifts. As a result, present-day species abundance and composition of many contemporary ecosystems does not resemble historical configurations (Hobbs *et al.* 2006; Hobbs, Higgs & Harris 2009). To date, most studies on the wider impacts of species gains or losses in ecosystems have focused on structural changes at the community level (e.g. changes in species abundance or diversity). Moving beyond describing shifts in community composition and structure and shedding light on how ecological reconfigurations alter the ecosystem functions and services on which human wellbeing depends is therefore a central challenge for ecology (Mooney *et al.* 2009). In the ecological literature, species' range shifts have received far less attention than species introductions or extinctions (Sorte, Williams & Carlton 2010), even though range shifts have been observed across a broad range of taxa and ecosystem types (Pecl & et al 2017). Given that

impacts of species range shifts on ecological communities may be similar in magnitude to those of introduced non-native species (Sorte *et al.* 2010), with successful range-shifting species sometimes displaying invasive properties (Engelkes *et al.* 2008), there is a clear and pressing need to explore the wider consequences of such shifts.

Anthropogenic climate change is one of the principal drivers of the contemporary reorganization of ecosystems (Pecl & et al 2017). Globally, species representing a wide range of taxa have responded to a changing climate by shifting their distributions to track more optimal conditions (Parmesan & Yohe 2003). Differences in the magnitude and pace of species' distribution shifts results in communities that are compositionally distinct from previous configurations, often called 'novel' or 'no-analog' communities (Williams & Jackson 2007; Hobbs *et al.* 2009). Generally, species have moved upwards and polewards in response to climate warming (Parmesan & Yohe 2003; Poloczanska *et al.* 2013), which has resulted in upland, temperate and austral/boreal habitats receiving an influx of species with warmer affinities than indigenous biota (García Molinos *et al.* 2015). Given that migrating and indigenous species often belong to different thermal realms (Stuart-Smith *et al.* 2015), a warming climate can result in competitive shifts, with warm-affinity species displacing or replacing cool-affinity ones (Lord & Whitlatch 2015; Warren II *et al.* 2016). Although such species replacements may cause no overall change in species richness, they may lead to considerable changes in ecosystem functioning—particularly if they involve species which exert strong control over ecosystem processes, such as dominant foundation species (Ellison *et al.* 2005).

In temperate marine systems, large, canopy-forming seaweeds (macroalgae) function as foundation species (*sensu* Dayton 1972), forming marine forests that provide biogenic habitat, alter local environmental conditions and mediate numerous ecological processes (Steneck *et al.* 2002; Teagle *et al.* 2017). Seaweeds are especially sensitive to climatic changes, and range shifts in response to past and contemporary climate variability are well described (Li, Hu & Duan 2016; Neiva *et al.* 2016; Straub, Thomsen & Wernberg 2016). The majority of contemporary seaweed range shifts have been

documented in temperate seas (Straub *et al.* 2016), where seaweed forests often dominate shallow rocky habitats. Temperate regions contain two distinct floristic elements, the cold- and warm-temperate (sensu Lüning, 1990), which differ in the temperature tolerances of the species they comprise. Climate change is driving shifts in the relative distribution of these elements, creating novel seaweed assemblages and with warmer-water species replacing colder-water ones, particularly in biogeographic transition zones (Lima *et al.* 2007; Tanaka *et al.* 2012; Fernández 2016). Although climate-driven reconfigurations of seaweed communities are well-documented (Harley *et al.* 2012), empirical evidence for their wider ecological consequences remains limited, and understanding how altered species composition affects ecosystem processes and functioning remains a persistent challenge (Pedersen *et al.* 2005).

Here, we examine whether the proliferation and predicted range expansion of a canopy-forming kelp with warm affinity will compensate for the decline and predicted loss of a morphologically similar—but less thermotolerant—cold-temperate species, which currently dominates across much of the shallow NE Atlantic rocky coastline. To understand how climate-driven changes in species composition may affect ecosystem functioning, we compared several core ecological processes linked to primary producers (biomass production, detrital flow, herbivory pressure and decomposition) between the two foundation species.

MATERIALS AND METHODS

Study species

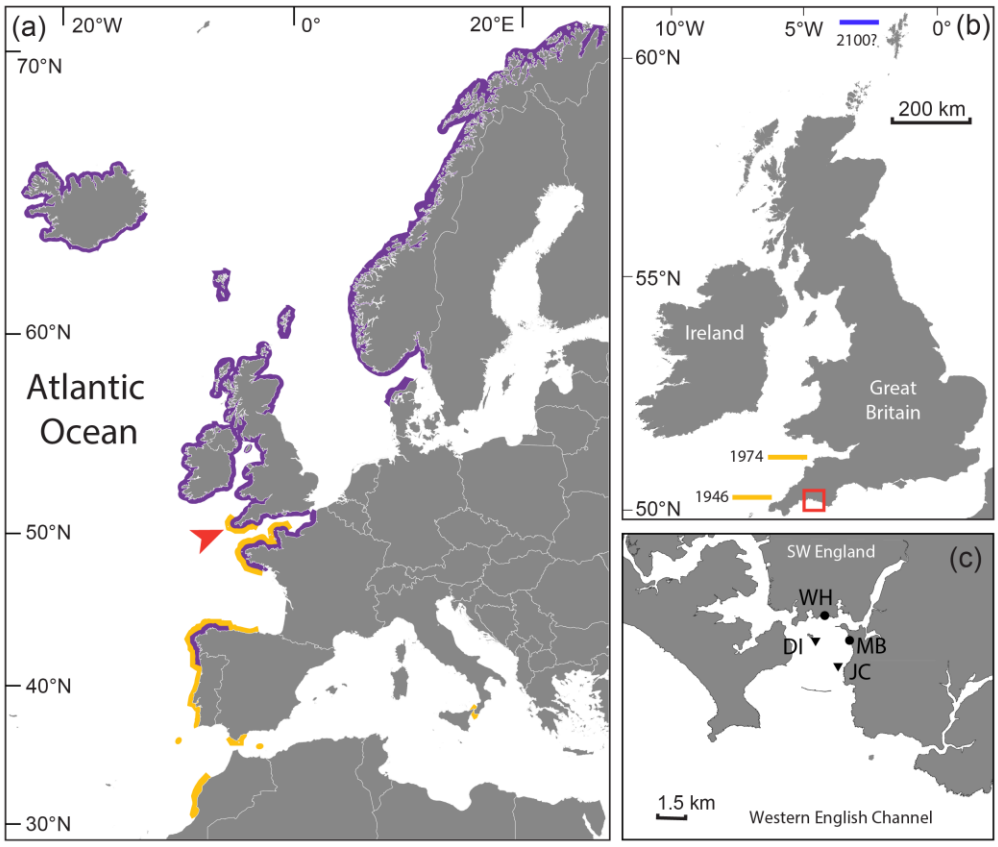
The kelp *Laminaria ochroleuca* is a warm-temperate species presently distributed from Morocco to southwest England in the United Kingdom (UK), where it was first detected in the late 1940s (Parke 1948) (Figure 1a, b). In recent decades, *L. ochroleuca* has increased in relative abundance at the leading-edge of its distribution (Smale *et al.* 2015; Teagle & Smale 2018), being now common throughout the southwest coast of the UK (Brodie *et al.* 2009) and dominating forest assemblages in many wave-sheltered locations (authors' pers. obs.). The growth and performance of *L. ochroleuca* is highly sensitive to temperature (Izquierdo, Pérez-Ruzafa & Gallardo 2002; Franco *et al.* 2017; Hargrave *et al.* 2017), and the recent proliferation of this species at the leading edge of its distribution has been linked to recent ocean warming (Smale *et al.* 2015; Teagle & Smale 2018). *L. ochroleuca* is predicted to continue expanding northwards in response to climate change, occupying most of the UK and large sections of the wider NE Atlantic coastline by the end of the century (Franco *et al.* 2017). The prospects for *L. ochroleuca* contrast with that of the cold-temperate kelp *Laminaria hyperborea*, the current assemblage dominant along moderate to wave exposed coastlines in the region. *L. hyperborea* does not perform well at high temperatures (tom Dieck (Bartsch) 1992; Wiencke *et al.* 1994), and over the past 40 years has undergone a ~250-km range contraction at its warm, trailing-edge on the Iberian Peninsula (Assis *et al.* 2016; Pereira *et al.* 2017). Continued ocean warming is expected to lead to further declines in abundance and shifts in its biogeographic distribution, with predicted extinctions of populations currently found along the coasts of Iberia, France and southern UK (Breeman 1990; Müller *et al.* 2009).

Study design and location

The stocks and fluxes of biomass are central to the biological, geochemical and physical processes that occur within kelp forest ecosystems, as well as in spatially-disconnected habitats subsidized by kelp-derived organic matter (Krumhansl & Scheibling 2012a). To investigate how future kelp forests

dominated by the warm-temperate kelp *Laminaria ochroleuca* might differ functionally from those formerly dominated by the cold-temperate *L. hyperborea*, we compared processes related to the cycling of organic matter between the two species in two mixed kelp forests. We estimated kelp biomass accumulation—a widely used proxy for kelp primary production (Krumhansl & Scheibling 2011; de Bettignies *et al.* 2013)—and biomass loss (detrital production) over the course of an annual cycle (March 2016–February 2017). Produced biomass can either (i) be directly consumed by grazers *in situ* or (ii) exported as detritus and later consumed by a vast array of microbes, detritivores, and suspension-feeders. To determine how biomass flows through grazing and detrital pathways in the coastal food web, we quantified the abundance of grazers associated with each kelp species and measured kelp detritus decomposition.

We used kelp forest ecosystems along the southwest coast of the UK—which currently represents the leading range edge of *L. ochroleuca*—as model study systems as this region is expected to experience major shifts in species composition and community structure in coming decades (Müller *et al.* 2009; Franco *et al.* 2017). Our study sites, West Hoe (hereafter 'WH') and Mount Batten ('MB') were located within Plymouth Sound (Figure 1c), and were characterised by dense kelp stands that extended from the low intertidal into the shallow subtidal zone. The first individuals of *L. ochroleuca* in UK waters were actually reported from that same area ~70 years ago (Parke 1948), allowing for sufficient time for kelp populations and associated biota to become established within these communities. The study sites are representative of moderately wave-exposed shallow rocky reefs in the region and both support mixed kelp canopies primarily comprising *L. ochroleuca* and *L. hyperborea*, the latter still being the assemblage dominant. Two additional subtidal sites were chosen to study kelp decomposition using litter bag experiments (see methodology below). Subtidal sites were chosen so the litter bags remained permanently submerged underwater.



156

157 **FIGURE 1.** (a) Approximate distribution of *Laminaria hyperborea* (purple line) and *L. ochroleuca*
158 (yellow line) along the NE Atlantic coastline. The red arrow indicates the study region, which is
159 shown in (b). *L. ochroleuca* was first detected in this region in 1946, and has since expanded its
160 distribution northwards. The dated yellow lines denote the position of the species leading range
161 edge. The blue line at the very top of (b) denotes the predicted range within the study region by the
162 end of the century, according to Franco *et al.* (2017). The sampling sites within study region (red box
163 in (b)) are shown in (c). The monthly sampling sites are denoted with a circle, the subtidal study sites
164 are denoted with a triangle. WH = West Hoe, MB = Mt. Batten, DI = Drake's Island, JC = Jennycliff.

165 *Biomass accumulation and loss*

166 Kelp biomass accumulation and loss was measured monthly using a modified hole-punch method
167 after Krumhansl & Scheibling (2011a). This technique consists of punching a series of holes at set
168 distances from the stipe/lamina transition zone, where the primary meristem occurs, to capture

growth of the lamina tissue. To obtain a growth estimate, hole-punched plants are retrieved after a certain time interval and the final position of the holes are measured. During spring low tides, 10–12 mature kelp plants (stipe length ≥ 20 cm) of each species were randomly selected, tagged and uniquely labelled at each site. Selected plants were from different areas of the forest each month. Two digits of each plant lamina were punched, and their initial length measured. Since growth is not uniform across the lamina (Kain 1976), a total of three holes were punched in every individual: two at 15 cm and 20 cm above the stipe/lamina transition zone on the central digit respectively, and another one at 20 cm above the aforementioned zone on an outer digit. The two holes punched on the central digit captured the maximal growth in length, which occurs between 2.5 and 15 cm from the central transition zone depending on the month (Kain 1976), while the hole on the outer digit captured variability in growth across lamina digits. After approximately one month, tagged kelps were harvested and returned to the laboratory for analysis. The final length of the punched digits, position of the holes, and the fresh weight of the stipe and lamina were recorded to calculate individual-specific lamina elongation and loss rates. The exact number of elapsed days between tagging and retrieval, as well as the number of tagged kelp plants relocated and retrieved, varied due to limited tidal windows and a rough sea state in some months. On average, > 8 individuals of each species were recovered from each site each month (see Table S1 and Table S2 in the Supporting Information for full details). In August however, bad weather hampered the retrieval of tagged plants. Given the low number of replicates (Table S2), and their small size compared to the plants tagged in the rest of the months (Figure S1), August data was not included in the analysis.

To convert elongation and loss rates of lamina tissue (cm) to gains and losses of fresh biomass (g), three 5 cm-wide segments from both the basal and distal parts of the lamina of each plant were cut across their width, cleaned of epiphytes, and weighed (fresh weight; FW). In order to make our results more comparable with those in the literature, we converted fresh biomass to dry biomass (DW). Every month and for each of the retrieved plants, we determined the relationship between fresh and dry weight (FW:DW) by drying one of the basal and distal segments at 60°C for 48 hours.

The basal and distal parts of the laminae were examined separately as the relationship can vary between different parts of the thallus (Smale *et al.* 2016). All relationships were highly significant and had an $R^2 \geq 0.85$. We then estimated the dry weight of the rest two segments from each part (out of the three we cut) using the calculated relationship. Finally, the measured and estimated dry biomass per unit length was averaged between all three segments to give the dry biomass per unit length ($g \cdot cm^{-1}$) of the respective basal and distal parts of the lamina (B_{base} and B_{distal}). This allowed us to convert elongation and loss rates of lamina tissue (cm) to accumulations and losses of biomass.

Biomass accumulation (BA) for each plant was estimated as:

$$BA = E \times B_{base} / t$$

where E is the average lamina elongation from the central and outer digits (denoted by a subscripted 1 and 2 respectively) obtained by subtracting the initial hole position at 15 or 20 cm from the final hole position (H_f):

$$E = \frac{[(H_{f1,1} - 15) + (H_{f1,2} - 20)] + (H_{f2} - 20)}{2}$$

and *t* denotes the days between the initial and final measurements (Table S1). The biomass loss (BL) was calculated as:

$$BL = M \times B_{distal} / t$$

where M is the average lamina loss obtained by subtracting the final length (L_f) of the central and outer digits from the sum of their initial length (L_i) and respective digit elongation (e) as follows:

$$M = \frac{[(L_{i1} + e) - L_{f1}] + [(L_{i2} + e) - L_{f2}]}{2}$$

In *L. hyperborea,* we observed a marked increase in the FW:DW ratio from June to September (Figure S2, Supporting Information), which was not documented for *L. ochroleuca* (Figure S2). During this period, the average biomass of the basal lamina segments was higher than the rest of the year (Figure S3). Regrettably, we could not account for the biomass accumulation that occurred during

these months, since our formula was based on elongation (i.e. linear growth; E), which was negligible from July to September (Figure S4). The observed biomass accumulation not related to linear growth was most likely explained by (i) the accumulation of carbohydrates, increasing the FW:DW ratio and (ii) increases in basal lamina thickness, which has been found to increase from July to December in *L. hyperborea* (Kain 1971, 1976). Although we did not measure changes in basal lamina thickness in our surveys, previous *L. hyperborea* studies have shown that there is an inverse relationship between relative changes in linear growth and thickness, with thickening being greatest when elongation rates are low (i.e. after June; Kain 1976). Our observations support such findings. As such, to account for *L. hyperborea* lamina thickening between June–September in our biomass accumulation formula, we used the minimal elongation rate recorded in the study (0.033 cm · day^{-1}) as a surrogate of lamina thickness growth during those months.

Grazer surveys

To explore how produced biomass is transferred to higher trophic levels via herbivory, we quantified the abundance of macroinvertebrate grazers associated with the laminae of *Laminaria hyperborea* and *L. ochroleuca* at our study sites over 13 months (March 2016–March 2017). Each month, 10 plants with comparable lamina areas of each species were randomly selected. The entire lamina of each individual was carefully placed into a large cotton bag and then cut from the stipe and the bag was then sealed to retain all grazers. In the laboratory, all macroinvertebrate grazers were identified and counted.

To examine the influence of kelp nutritional quality in determining the herbivory pressure patterns observed in the field, we used a series of feeding preference assays using artificial diets (Hay *et al.* 1998). Fresh kelp plants were harvested in April 2016, the central and distal sections of the laminae cut into strips and subsequently freeze-dried. Kelp strips were then pulverized to a fine powder using an electric grinder and stored in a freezer. We prepared a seaweed solution containing 1 g of kelp powder, 1 g of pulverized *Ulva sp*. and 20 ml of water. *Ulva sp.* was added to the mix as kelp

243 alginates made the solution too viscous, and *Ulva spp*. are less chemically defended than brown
244 algae (Duffy & Hay 1994). Agar (0.7 g) was added to a further 20 ml of water, heated to boiling point,
245 and quickly homogenized with the seaweed solution. This final mixture was then poured onto a glass
246 plate covered in microscope slides with 1×1 mm plastic mesh glued on top. Finally, another glass
247 panel was rapidly placed on top, sandwiching the mesh-covered slides and spreading the algal
248 mixture to a uniform 1-mm thickness on all slides. After 2 min, the solidified mixture had adhered to
249 the mesh slides, which were individually cut using a razor. We used the gastropod *Gibbula cineraria*
250 as a model grazer for our laboratory experiments as it was frequently observed on kelp laminae, and
251 was the largest grazer recorded in our surveys (see Results). Macroinvertebrate grazers like *Gibbula*
252 spp. can feed directly on kelp tissue or indirectly on the associated biofilms and epiphytic algae.
253 Kelp-derived organic matter can contribute significantly to the diet of *Gibbula* spp. (Leclerc *et al.*
254 2013), whose grazing activity leaves evident grazing marks on the kelp blades (authors' pers. obs.),
255 further suggesting that kelp organic matter is ingested. *G. cineraria* individuals were collected locally
256 and were starved for 3 days in large aerated tanks (allowing for emptying of the digestive tract),
257 before being transferred to smaller (20 × 8 × 10 cm) rectangular tanks for feeding trials. A single
258 individual was placed in the middle of the rectangular tank, which contained one slide of *L.*
259 *ochroleuca* and one slide of *L. hyperborea* agar mixture positioned at opposite ends. An air stone
260 with low air flow was also placed in the middle of the tank. We determined kelp consumption by
261 counting the number of squares that been consumed after 48h. Fourteen replicate trials were
262 conducted simultaneously.

263 *Kelp decomposability*

264 To investigate how kelp biomass is consumed and recycled once it has been cast as detritus, we
265 compared rates of detritus decomposition between the two kelp species. Lamina material from each
266 species was collected and cut into strips (ca. 5 × 15 cm). A total of 105 ± 8 grams of fresh kelp strips
267 from the same region of the laminae was then sealed within mesh bags (mesh aperture 20 mm),
268 which were uniquely labelled. The mesh size allowed mesodetritivores and microbes to access the

kelp detritus whilst minimizing loss of material via flushing. Four replicate bags for each species were deployed at a depth of 4 m (below Chart Datum) by scuba divers at Drake's Island and Jennycliff, both within Plymouth Sound (see Figure 1c) in March 2016. Litter bags were attached to a long rope (positioned ~1 m apart from one another), which was secured to the seabed with anchor weights. Bags were deployed on a sandy seabed adjacent to a kelp-dominated rocky reef and were retrieved after 40 days. Upon retrieval, a fine mesh bag (1µm diameter) was placed over each litter bag to retain all kelp material and detritivores, before detaching the bag from the rope. In the laboratory, the contents of the bags were carefully removed and washed through a 1 mm sieve. Remaining fresh kelp tissue was reweighed again to assess degradation rates ($g \cdot day^{-1}$), and the abundance of detritivores associated with the kelp material was quantified.

Kelp habitat structure

The measurements described above were mostly collected at the scale of individual plants (i.e. per capita). In order to contextualise our findings at larger spatial scales (i.e. per unit area) and increase generality, we conducted ecological surveys of kelp-dominated habitats within the study area to determine whether both foundation species can occur at similar densities. We surveyed a number of subtidal and intertidal reefs within the study region by haphazardly placing 10 replicate 1 m^2 quadrats and quantifying the density of mature canopy-forming plants of each species.

Statistical analyses

Differences in biomass accumulation and loss ($g \cdot day^{-1}$) between kelp species (2 levels, fixed factor), sites (2 levels, fixed factor) and months (11 levels, fixed factor), were examined with permutational ANOVA (Anderson 2001) due to observed structuring of residuals and heterogeneity of variances encountered in exploratory analyses. August data were excluded from analyses as explained above (see Table S2 and Figure S1). For each response variable, we generated a similarity matrix based on Euclidian distances with untransformed data using PRIMER (v7.0) software (Clarke & Gorley 2015) with the PERMANOVA add-on (Anderson, Gorley & Clarke 2008). Main effects and interactions were

294 then tested with 9999 permutations under a reduced model. Where significant differences were
295 recorded (usually $p<0.05$ but see below) we conducted *post-hoc* pairwise tests between levels of
296 factors (or within levels of factors for significant interaction terms). While permutational ANOVA is
297 more robust to non-normal distributions and heterogeneity of variance than traditional ANOVA, it is
298 still influenced by differences in dispersion between treatments. To examine data dispersion, we
299 conducted PERMDISP tests to determine whether within-group variation differed between levels of
300 each factor. Where a significant difference in dispersion was recorded, the p-value of the associated
301 PERMANOVA test was reduced a more conservative $p<0.001$.

302 To test for differences in abundance of the dominant grazers *Gibbula cineraria* and *Patella pellucida*
303 between kelp species (2 levels), sites (2 levels) and months (13 levels, March 2016–March 2017), we
304 performed the same analysis as outlined above. In the feeding preference experiments with *Gibbula*
305 *cineraria*, we used a paired Wilcoxon rank-sum test to test for differences in kelp consumption
306 between species, as pairwise differences did not follow a normal distribution.

307 Finally, for the decomposition experiment, we used a univariate permutational ANOVA to test for
308 differences in kelp degradation rates ($g \cdot day^{-1}$) between species and sites (2 levels each, fixed
309 factors). We generated a similarity matrix based on Euclidian distances and examined variability
310 between factors with 9999 permutations under a reduced model.

311 RESULTS

312 *Biomass accumulation and loss*

313 Across our year-long study, we retrieved a total of 197 *Laminaria ochroleuca* and 204 *L. hyperborea*
314 plants for biomass accumulation and loss determination. Biomass accumulation rates exhibited
315 marked seasonality and differed considerably between species and sites (Figure 2a, Table S3). We
316 also recorded a significant 3-way interaction between species, month and site (Table S3). Further
317 examination of variability patterns showed that seasonality in biomass accumulation differed

between species, but the magnitude of dissimilarity was not entirely consistent between sites (Figure 2a). Overall, we recorded a significant main effect of species and *L. ochroleuca* plants accumulated more biomass, producing an annual average of 123.8 ± 18.9 g DW yr^{-1} and 137.1 ± 13.5 g DW yr^{-1} (means ± standard error, SE) at WH and MB respectively, which was ~80 and ~90% more than the average 69.9 ± 6.3 g DW yr^{-1} and 72.4 ± 4.0 g DW yr^{-1} produced by *L. hyperborea* plants. *L. ochroleuca* exhibited continuous growth throughout the year, steadily increasing lamina biomass until peak production around the onset of summer (0.63 ± 0.05 g DW d^{-1} in May at WH and 0.62 ± 0.04 g DW d^{-1} in June at MB). Biomass accumulation started gradually declining after June, with growth remaining relatively consistent at around 0.2−0.3 g DW d^{-1} between September and January; the lowest biomass accumulation was recorded in November (0.09 ± 0.02 and 0.24 ± 0.02 g DW d^{-1} at WH and MB on average, respectively). Contrastingly, *L. hyperborea* biomass accumulation was markedly discontinuous; plants showed a distinct growth phase from December to June and a resting phase from July to November, during which lamina elongation was negligible (Figure S4) but increases in lamina mass and thickness occurred. Peak growth occurred in mid-spring at both sites (April: 0.87 ± 0.03 and 0.78 ± 0.04 g DW d^{-1} at WH and MB respectively).

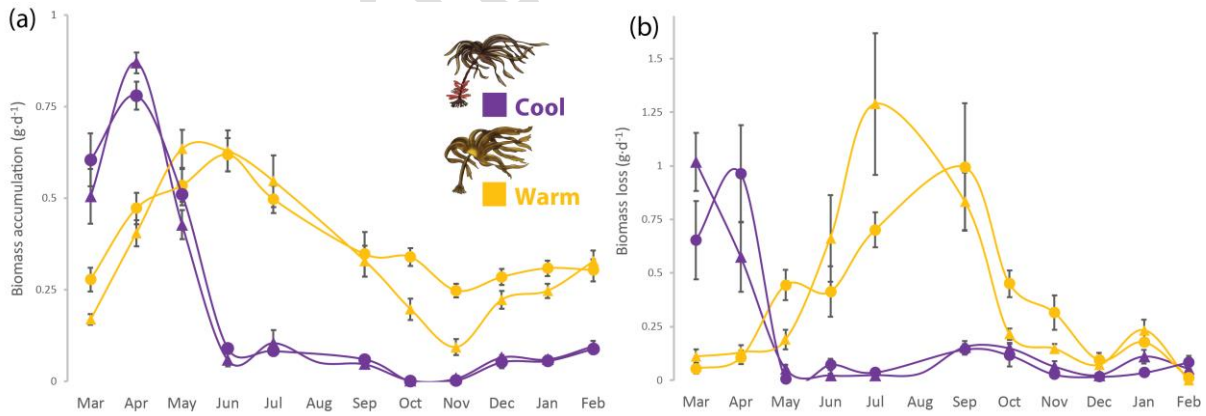


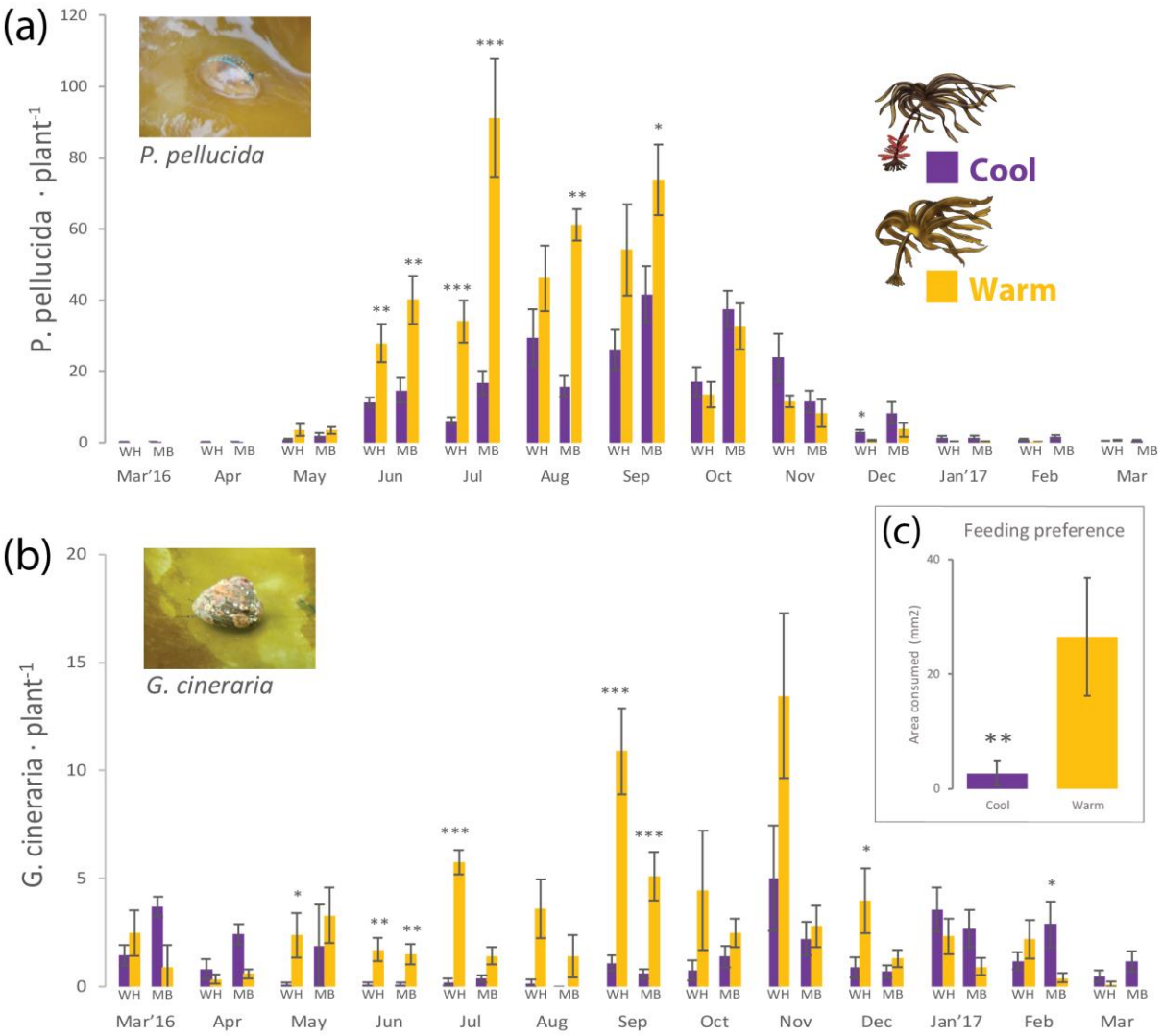
FIGURE 2. Annual patterns of (a) lamina biomass accumulation and (b) loss of the cool-temperate kelp *Laminaria hyperborea* (purple lines) and the warm-temperate congener *L. ochroleuca* (yellow lines) in mixed kelp forests at West Hoe (triangles) and Mount Batten (circles). Markers denote means ± standard error (SE). Data from August was excluded from analyses due to low replication.

Loss rates of lamina biomass were consistent among sites, but varied significantly between months and species (Table S3). We recorded a significant 3-way interaction between species, months and sites (Table S3). Further examination of variability patterns showed that seasonality in biomass loss differed between species, but the timing of peak biomass loss differed slightly between sites (Figure 2b). *L. ochroleuca* biomass loss occurred throughout the year, with the maximum detrital production recorded between June and September (1.29 g ± 0.33 DW d^{-1} and 0.99 g ± 0.30 DW d^{-1} maximum loss in July at WH and in September at MB, respectively). Annual detritus production via lamina loss totalled 122.4 ± 13.4 g DW yr^{-1} and 120.4 ± 11.1 g DW yr^{-1} for *L. ochroleuca* and 69.7 ± 6.7 g DW yr^{-1} and 66.9 ± 9.3 g DW yr^{-1} for *L. hyperborea* at WH and MB, respectively. In contrast to *L. ochroleuca*, *L. hyperborea* biomass loss peaked at the beginning of spring (1.02 ± 0.14 g DW d^{-1} in March at WH and 0.96 ± 0.22 g DW d^{-1} in April at MB), when the collar of old growth produced during the previous season—which had remained attached to the newly-formed meristematic lamina tissue—was cast. After April, lamina biomass loss decreased to near-zero, and remained constant between 0.02–0.15 g DW d^{-1} for the rest of the year.

Grazer surveys

Only two species of macroinvertabrates, the blue-rayed limpet *Patella pellucida* and the trochid gastropod *Gibbula cineraria,* were found grazing on kelp laminae. Across the 13-month-long field study, we recorded a total of 4369 *Patella pellucida* individuals on *L. ochroleuca* and 2439 individuals on *L. hyperborea*. Overall, *Laminaria ochroleuca* supported significantly higher abundances of *P. pellucida* than *L. hyperborea* (Table S3, Figure 3a). *P. pellucida* occurred on kelp laminae year-round, but exhibited high seasonality in abundance patterns. Both *L. ochroleuca* and *L. hyperborea* supported very few *P. pellucida* individuals (between 0 and 3.5 ± 0.8 limpets per plant) until June, after which abundances markedly increased (Figure 3a). The highest abundance of limpets on *L. ochroleuca* was recorded in July and September (91.3 ± 16.5 and 54.1 ± 12.8 individuals, at MB and WH, respectively), whereas limpets were most abundant on *L. hyperborea* in August and September (41.6 ± 7.9 and 29.5 ± 7.9 individuals at MB and WH, respectively). We recorded a significant 3-way

365 interaction as seasonal patterns of abundance differed between species but the magnitude of
366 dissimilarity between species was generally higher at one of our sites (MB; Figure 3a).
367
368 We recorded a total of 685 *Gibbula cineraria* individuals on *L. ochroleuca*, compared to 363 on *L.*
369 *hyperborea*. Overall, *L. ochroleuca* supported higher abundances of *G. cineraria* (Table S3, Figure 3b).
370 The abundance of *G. cineraria* on *L. hyperborea* was generally low, with <1 individuals present
371 throughout the summer months at both sites, on average (Figure 3b). Abundance values were
372 slightly higher in winter but did not exceed 5 ± 2.4 individuals per plant and were fairly consistent
373 across months (Figure 3b). Conversely, the abundance of *G. cineraria* on *L. ochroleuca* laminae was
374 highly variable between months, often registering two-fold or three-fold differences between
375 consecutive months. Maximum abundance values were recorded in November (13.4 ± 3.8 and 5.1 ±
376 1.1 individuals at WH and MB, respectively). Statistically, we detected a significant interaction
377 between species and month, as the magnitude of dissimilarity between species was greater during
378 summer months (Figure 3b). In the feeding preference trials, *G. cineraria* exhibited a strong
379 preference for *L. ochroleuca* over *L. hyperborea* (W = 179.5, p-value <0.001), with average
380 consumption rates being an order of magnitude greater on the warm-water species (Figure 3c).
381



382

383 **FIGURE 3.** Abundance of the grazers *Patella pellucida* (a) and *Gibbula cineraria* (b) on the laminae of

384 the cool-temperate kelp *Laminaria hyperborea* (purple bars) and the warm-temperate congener *L.*

385 *ochroleuca* (yellow bars) in mixed kelp forests at West Hoe (WH) and Mount Batten (MB). Results

386 from the feeding preference experiments with *G. cineraria* (n=14) are shown in (c). Bars represent

387 mean values ± SE.

388

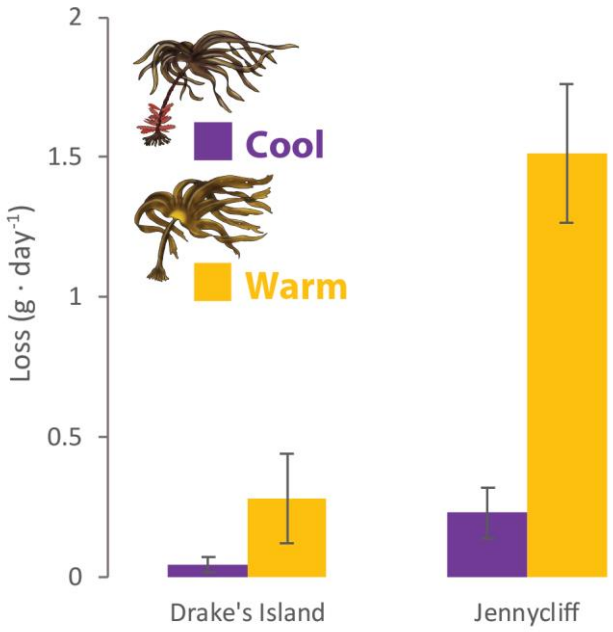
389 *Kelp decomposition*

390 In the litter bag experiment, decomposition rates of *Laminaria ochroleuca* were consistently higher

391 than *L. hyperborea* (Figure 4). We recorded a significant interaction between species and site (Table

392 S4) as the magnitude of differences between species varied between sites, with relatively lower loss

393 rates of *L. ochroleuca* at Drake's Island compared to Jennycliff (Figure 4). After the 40-day
394 deployment, the fresh weight of *L. ochroleuca* had decreased by 56.9% and by 10.5% at Jennycliff
395 and Drake's Island respectively, whereas *L. hyperborea* biomass declined by 8.9% and just 1.6% at
396 the same sites. The structure of detritivore assemblages associated with kelp matter (which were
397 numerically dominated by amphipods and isopods) was highly variable, and did not vary significantly
398 between kelp species (Table S4).



399

400 **FIGURE 4.** Kelp decomposition rates for the cool-temperate *Laminaria hyperborea* (purple bars) and
401 the warm-temperate congener *L. ochroleuca* (yellow bars) at two subtidal study sites.

402 *Kelp habitat structure*

403 The densities and relative abundances of canopy-forming *Laminaria hyperborea* and *L. ochroleuca*
404 plants varied between sites (Table S5). Crucially, however, the total density of kelp plants was
405 broadly similar across sites, regardless of the proportional representation of each species. Indeed,
406 plant densities at sites dominated by *L. hyperborea* were similar, albeit slightly higher, to those at
407 sites dominated by *L. ochroleuca* (Table S5).

DISCUSSION

Our results reveal fundamental differences in several processes central to ecosystem functioning (biomass production, detrital flow, herbivory and decomposition) between two foundation species with contrasting thermal affinities. These findings suggest a substantial shift in the cycling of organic matter within the forests of the study region following the replacement of a cold-temperate species by a warm-temperate one, and provide rare evidence of how range shifts and species substitutions can affect ecosystem functioning in marine ecosystems. Despite being taxonomically related and morphologically similar to the cool-temperate *Laminaria hyperborea*, the warm-temperate kelp *L. ochroleuca* was ~1.8 times more productive and generated ~1.8 times more detritus via lamina erosion, resulting in a larger pool of organic matter entering detrital food webs (Figure 5). Given that the warm-temperate species supported greater numbers of grazers and was a preferred food source, the proliferation of this kelp into cool-temperate communities will also likely alter trophic pathways within kelp forests (and potentially beyond) by increasing the amount of production that enters higher trophic levels via herbivory (Figure 5). It is yet unclear how other consumers of kelp-derived organic matter (e.g. suspension feeders and deposit feeders) might be affected, and whether the changes we document here will extend to secondary consumers (Figure 5, dashed arrows). However, given the magnitude of the changes we report, it seems unlikely that effects will be negligible. Finally, the higher detritus decomposability of warm-temperate plants will increase nutrient turnover and decrease the residence time of kelp detrital exports, potentially affecting trophic connectivity between kelp forests and other habitats (Figure 5).

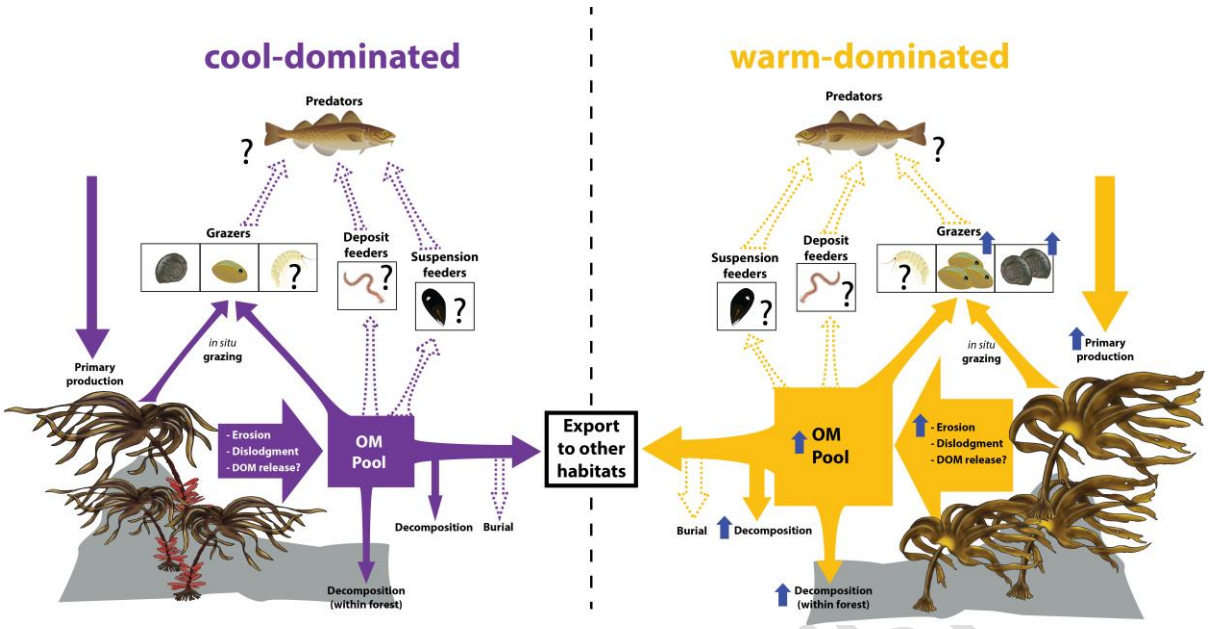


FIGURE 5. Schematic representation of the expected fluxes of kelp organic matter as some kelp forests within the study region transition from being dominated by cool- to warm-temperate foundation species. Blue arrows indicate changes in the processes measured; question marks and dashed, empty arrows denote mechanisms and pathways that were not evaluated in this study. Results suggest that, in forests dominated by the warm-temperate species, a larger fraction of kelp-derived matter may be consumed by grazers (principally snails, limpets and amphipods), which can feed directly on the standing or dislodged plants. Warm-temperate plants produced larger amounts of detritus, thus creating a large pool of organic matter (OM). That pool is either (i) consumed by suspension and/or deposit feeders, (ii) decomposed by microbes or (iii) exported to other habitats, where it may be consumed/decomposed or eventually buried. Detritus from warm-temperate plants decomposed much faster, which may affect the fate of the OM pool and/or its export. The kelp organic matter assimilated by primary consumers may flow to higher trophic levels via predation.

The warm- and cold-temperate kelps exhibited markedly different growth strategies, which can explain the differences in total annual biomass accumulation to some extent. The warm-temperate species showed continuous growth and erosion of the lamina throughout the year, providing a steady supply of particulate organic matter and essentially acting as a “conveyor belt” of biomass

447 accumulation and detritus production. Conversely, the growth strategy of the cool-temperate
448 species was characterized by discrete phases, with a distinct growing phase and an intense period of
449 detrital production during the casting of the old lamina growth, which remains attached to the newly
450 growing lamina until March−May (Kain 1971). The cool-water species is considered a "season
451 anticipator" (sensu Kain 1989) as its growth is controlled by a strategic annual rhythm (Schaffelke &
452 Lüning 1994), and shows little response to environmental conditions. In contrast, the growth
453 strategy of the warm-temperate species is characteristic of a "season responder", with growth rates
454 closely correlated with irradiance levels (Kain 1989).
455
456 Such fundamental differences in growth strategies—and the consequent temporal alterations to the
457 production and release of organic matter—are likely to translate into wider changes in the way
458 energy and nutrients flow through grazing and detrital pathways in the coastal food web. A greater
459 amount of kelp production will enter the food web via direct grazing, as evidenced by the warm-
460 water kelp supporting greater densities of the grazer *Gibbula cineraria* and being a preferred food
461 source. A similar pattern was found for the tiny limpet *Patella pellucida*, which feeds almost
462 exclusively on kelp (Leclerc *et al.* 2013; Hereward *et al.* 2018). The contrasting grazer preference
463 between kelp species could relate to differences in their biochemical composition, which influences
464 food palatability and nutritional quality. As variability in grazer preferences can influence the
465 ecological performance and population structure of seaweed species (Duffy & Hay 2000), the
466 interspecific variability we recorded here may have implications for the population dynamics of
467 these habitat-forming kelps. Grazers can exert considerable influence upon macroalgal assemblages
468 (Hay 1991) especially at early stages of algal development (Korpinen et al. 2007), and relationships
469 between grazers and their host algae are pivotal in characterising community organization (Duffy &
470 Hay 2000) and ecosystem functioning (Bruno et al. 2008). However, compared with many other algal
471 groups, herbivores generally consume a relatively low proportion of kelp primary production

(Krumhansl & Scheibling 2012b), particularly when the primary grazers are small in size—as is the case with the current study region (Smale *et al.* 2013, 2016; Hereward *et al.* 2018).

Indeed, more than 90% of the biomass accumulated in the laminae of tagged plants was lost as eroded fragments in both kelp species, providing further evidence that the vast majority of kelp primary production enters the detrital food web (Krumhansl & Scheibling 2012b). The continuous and considerably larger supply of detritus generated by the warm-temperate kelp will provide a larger pool of organic matter available to consumers such as deposit- and suspension-feeders. This pool is an important food source for consumers both within the kelp forest but also within spatially-disconnected habitats such as seagrass meadows or sedimentary substrates, where kelp organic matter constitutes an important trophic subsidy (Vanderklift & Wernberg 2008; Abdullah, Fredriksen & Christie 2017; Figure 5). Interestingly however, we found that detritus from the warm-temperate species decomposed an average of 6.5 times faster than that of the cool-temperate one; this may decrease detritus residence time and its availability for long-range transport, thus affecting trophic connectivity between kelp forests and other habitats. Changes in the magnitude and identity of detrital subsidies can also alter the structure of kelp detritivore communities (Bishop, Coleman & Kelaher 2010), as documented after the arrival of invasive species (Taylor *et al.* 2010). Although we did not find significant differences in the abundance of detritivores between our mesh bags, further work is required to examine how the composition of detritivore assemblages will be influenced by the continuous—but ephemeral—supply of *L. ochroleuca* detritus. Determining whether changes in the abundance of detritivores and grazers—which are important prey items for fish and crustacean predators (Muntz, Ebling & Kitching 1965; Norderhaug *et al.* 2005)—will impact higher trophic levels should also be a priority for future research.

Despite the observed contrasting biomass dynamics between the kelp species, some of the key ecosystem functions and services delivered by kelps in the NE Atlantic will likely persist in the future,

as several ecological processes were maintained or even enhanced. For instance, kelp forests dominated by the warm-temperate species will still exhibit high rates of carbon capture, as plant primary production—and therefore carbon assimilation—was higher than that of the cool-water kelp. Both species are also morphologically similar and form canopies of similar heights and plant densities (Smale et al. 2015; Table S5) and, as such, kelp forests dominated by the range-expanding species are likely to continue to provide habitat for wide range of fish, invertebrate and algal species (O'Brien *et al.* 2018; Teagle *et al.* 2018). That said, recent work has shown that the epibiotic assemblages associated with kelp stipes, which are typically dominated by red seaweeds and sessile invertebrates, are less diverse in the warm-temperate species (Teagle & Smale 2018). The future of NE Atlantic kelp forests contrasts with that in other marine temperate regions where, in many cases, ecological functions provided by kelps have not been replaced following their decline, as they have been superseded by structurally-dissimilar algae (Terazono *et al.* 2012; Dijkstra *et al.* 2017) and even completely different foundation species such as corals (Vergés *et al.* 2014). For example, gradual ocean warming and discrete marine heatwaves have resulted in structurally-complex kelp forests being replaced by low-lying, architecturally-poor habitats dominated by turf-forming algal species in several regions across the globe (Filbee-Dexter & Wernberg 2018). Since the ecological characteristics of algal turfs differ markedly from those of larger canopy-forming seaweeds, such replacements can lead to substantial reductions in associated biodiversity (Smale & Wernberg 2013; Cheminée *et al.* 2017) and alterations to key functions such as net primary productivity (Copertino, Connell & Cheshire 2005). Similarly, the introduction of non-native seaweeds with traits differing from those of kelps modified the trophic dynamics and the circulation of organic matter within recipient marine ecosystems (Pedersen *et al.* 2005; Dijkstra *et al.* 2017). Such shifts in the structure and functioning of marine forests have major implications for human societies. For instance, the climate-driven loss of kelp forests from the temperate coasts of Japan culminated in a dramatic decline in kelp-associated abalones and, ultimately, the crash of one the most important fisheries in the region (Serisawa *et al.* 2004; Kiyomoto *et al.* 2013).

The magnitude of change in NE Atlantic kelp forests as waters continue to warm will partly depend on whether the warm-temperate kelp can entire replace its cold-affinity congener as it retracts polewards. While the warm-temperate kelp attained similar densities to those the cold-water species and even dominated kelp forest assemblages in the surveyed sites within moderate to low wave exposure, it was less abundant in wave exposed locations (Table S5). This is likely because *L. ochroleuca* is more susceptible to being dislodged by wave action (Smale & Vance 2015). Interestingly however, within recent decades this species has extended its distribution from sheltered on to moderately wave-exposed locations (Smale *et al.* 2015). The broadly comparable densities we found at our survey sites thus suggest that the plant-level differences we report here will broadly scale up to larger spatial scales at the ecosystem level, at least in sheltered moderately wave-exposed coasts. Further, the central NE Atlantic contains a rich diversity of canopy-forming seaweeds, and it remains to be seen whether other kelp species with warmer affinities than *L. hyperborea* (e.g. *Saccorhiza polyschides*) may play a more influential role within kelp forest habitats in the future. Contrastingly, kelp forests in regions with fewer foundation species and with lower functional redundancy may be more vulnerable to ecosystem shifts. For instance, an extreme warming event led to the loss of extensive areas of kelp forests in Australia—which are dominated by a single species of kelp—fundamentally altering ecosystem dynamics and forcing a regime shift to algal turfs (Wernberg *et al.* 2016). It is also likely that kelp-dominated habitats located towards the warm-water limit of the kelp species' distributions are more vulnerable to ocean warming, and are more susceptible to radical shifts in canopy structure and consequent loss of core ecosystem functions (Raybaud *et al.* 2013; Wernberg *et al.* 2016).

Climate change has resulted in an upward and poleward migration of warm-affinity species, which often displace and replace cold-affinity ones (Peñuelas & Boada 2003; Beck *et al.* 2011; Warren II *et al.* 2016). *Laminaria hyperborea* forests are currently the dominant vegetation type along much of

the NE Atlantic coastline, with an estimated spatial extent of ~18,000 km^2 (Pessarrodona *et al.* 2018). As a consequence of ocean warming, this species is predicted to lose between 8.41% and 39.44% of its entire suitable habitat by the end of the century, as moderate expansions at its northern poleward range edge will not compensate for extensive losses further south (Assis *et al.* 2016). Our findings suggest that the predicted expansion (Franco *et al.* 2017) of a warm-temperate congener into habitat formerly dominated by *L. hyperborea* will likely result in noticeable shifts in the magnitude and flow of organic matter in NE Atlantic kelp forest ecosystems and interconnected nearshore habitats. Even so, these novel forest communities could potentially preserve some of the key ecosystem functions and services delivered by current kelp-dominated habitats. Our work demonstrates that, like species invasions (Mascaro, Hughes & Schnitzer 2012), climate-driven shifts in species composition can maintain or even enhance ecosystem processes to some extent, and suggests that the impact of species replacements will depend, to some degree, on the similarity in functional traits between climate change 'winners' and 'losers'. Overall, our findings point to the need to consider functional traits over species identity when examining the wider impacts of human-mediated shifts in species composition on ecosystem processes, functions and services.

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AUTHOR CONTRIBUTIONS

All authors contributed to the development of ideas, interpretation of results, and writing of the manuscript. AP led fieldwork, sample collection and processing, and data analysis. AF orchestrated

574 the feeding preference assays and provided valuable advice. DS originally conceived the study and
575 co-wrote the first draft of the manuscript with AP.

576 DATA ACCESSIBILITY

577 Data is deposited in the Dryad Digital Repository (doi:10.5061/dryad.1d9p080)

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